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Studies in the genus Taraxacum

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(WITH PLATES 6 AND 7)

LOSS OF SEXUALITY IN TARAXACUM

The genus *Taraxacum* presents some interesting problems—taxonomic, cytological and genetical. The classical castration experiments by Raunkiaer (7) in 1903 showed the common dandelion, *T. vulgare* (Lam.) Schrk. (*T. officinale* Weber), to be capable of setting viable seeds without pollination. Since Schwere (10) had previously described the development of the embryo from the egg cell, the condition was spoken of as "parthenogenesis," and Raunkiaer concluded that all species of *Taraxacum* were parthenogenetic. This was questioned by Dahlstedt (2) in 1907, and two years later Rosenberg (9) showed *T. confertum* to be normally sexual. Likewise, Ikeno and Osawa (6) showed that of two species growing side by side in Japan, *T. platycarpum* Dahlst. and *T. albidum* Dahlst., the former is normally sexual while the latter requires no pollination for the production of viable seeds.

Up to 1915 two careful studies had been made as to megasporogenesis and other cytological features in the genus: that of Juel (5) on *T. vulgare* and that of Osawa (6) on the two aforementioned Japanese species. At that time it was suggested to the writer by Professor D. M. Mottier that species of *Taraxacum* growing in America ought to be investigated. Accordingly, in the spring of that year, the writer commenced the study of the genus and was able to confirm the cytological work of Juel on

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T. vulgare. Several varieties of our common dandelion found growing in southern Indiana were drawn into the study, and although the material was selected from different varieties, the numerous preparations showed no differences in cytological behavior.

A second species, *T. erythrospermum* Andrz., has extended itself westward and finds a fairly general distribution throughout the middle western states. The sporogenesis of this species was likewise studied and the details of its megasporogenesis are given under a separate heading in the third part of this paper.

Meantime, numerous castration experiments after the manner first employed by Raunkiaer (7) were applied to plants of several varieties of *T. vulgare* and of *T. erythrospermum.* The object here was to determine whether all these forms set viable seeds in the absence of pollination and whether these show the same percentages of viability as seeds normally developed. The latter species had not been investigated in this respect up to that time. Raunkiaer had included a "*T. erythrospermum*" in the list of plants studied by him, but Dahlstedt (2) says that under this name was meant *T. laetum* Dahlst. Since that time Sears (11) has reported similar studies before the Ohio Academy of Science. In the experiments the excised part of each head was examined to make sure that the anthers were all closed and completely removed together with the stigmata. If this was not the case the entire head was discarded from the experiment. When a head was chosen that was too young, the result was that it dried up from too rapid a loss of moisture from the cut surface, especially in drying weather. It was therefore necessary to select heads at as late a stage as possible but before the opening of the loculi of the anthers. When these precautions were taken, the heads in all cases developed achenes altogether normal in appearance. Germination tests were made with seeds so produced and those produced in heads not castrated that grew by their side, in each case on the same plant. The seeds of *Taraxacum* will germinate immediately after they are mature. The results of these tests indicated no difference in viability between seeds normally developed and those from castrated heads.

Incidentally it may be said that seed formation in *Taraxacum* *vulgare* is not easily interfered with. A small percentage of viable seeds were found in heads that had been cut down at the time of their flowering and left to lie in the grass. And if flower heads with their long scapes attached were cut from the plant and put under a bell jar in the laboratory, the achenes would complete their development and a small percentage showed germinability.

The question naturally followed, does normal fertilization ever take place in these species? The pollen of the two species shows great variation in size even within the same anther. In its development it shows such abnormalities as are often seen in the pollen formation of sterile hybrids. The degree of this abnormality varies in different plants. Numerous examinations of stigmata with pollen adhering to them were made under magnification for evidence of pollen tubes. None were ever observed in either species. The media used by various workers to induce the germination of pollen were employed in an effort to produce pollen tubes, but without result. Finally, numerous pistils, collected at a time just before their wilting, were fixed, embedded in paraffine in bundles of fifteen to twenty and sectioned for a short distance from the stigmatic end. After staining, careful examination revealed no trace anywhere of an invading pollen tube. All this, to be sure, cannot be considered conclusive evidence that the pollen does not germinate and that fertilization never takes place in *T. vulgare* and *T. erythrospermum*, but it points toward that conclusion. In this connection, Dahlstedt (2) expresses the opinion that in species generally "apogamous" there may occur single embryos arising normally from a fertilized egg. He refers to the results of Rosenberg (8), who found in the same head of a *Hieracium* "Apogamie" as well as fertilization.

It was found, as will appear in the cytological part of this paper, that there is no reduction division in the course of megasporogenesis. Enough embryological preparations were made to show that the embryo develops—at least usually, for it was true in all observed cases—from the unfertilized egg, which retains the $2x$ chromosome number. In a sense, it is an inaccuracy to call this cell an egg, for it lacks the character of a true egg of having the haploid chromosome number. For the same reason the term parthenogenesis cannot well be applied unqualifiedly to such a case. The term apogamy, so far as its inherent meaning goes, applies, but this term has received a special significance by being applied to embryo-origin from a vegetative cell. Both terms are therefore objectionable, and the difficulty is due to the fact that the embryo starts from a cell that partakes of some of the characters of an egg and some of the characters of a vegetative sporophyte cell, more especially its diploid chromosome number. An arbitrary compromise was therefore reached by Winkler (12) in the adoption of the expression, "somatic parthenogenesis." It would seem to the writer much more logical to qualify the meaning of the term parthenogenesis by the use of the more specific adjective, diploid, instead of by the general adjective, somatic, for it is only that one character of a somatic cell, the possession of a diploid chromosome number, which one wishes to emphasize in connection with this type of apomixy. In all its other characters it certainly is not somatic. Sears (11) has coined the expression "amiotic parthenogenesis," The writer would characterize the condition either by the term "parthenogenesis" modified by an adjective, as "diploid" or "amiotic" or by the term, "ooapogamy." The latter term has been used, but the writer is at present unable to determine who is responsible for the expression.

Since the embryos of the two species of *Taraxacum* in question arise through ooapogamy, the reduced chromosome number does not enter into the life cycle of these plants and amphimixis is wanting. For this reason they suggested themselves as good objects for the study of certain genetical problems. Here the question of hybridization is completely shut out at the present stage in their evolution. It is possible that there was considerable hybridization at one time in the phylogeny of the genus. We must accept such a conclusion if we believe that polymorphy is the result of early hybridization. Did the ooapogamous species lose their normal sexuality independently of one another after they had arisen through hybridization, or did this loss occur in a single species, which is then the parent species from which were evolved the present-day ooapogamous species? Perhaps the latter of the two alternatives would seem the more likely, which would then mean that mutation had played a part in their production in the absence of hybridization. Dahlstedt

(2) remarks that "probably quite likely the genus has at one time been and is still perhaps in a period of mutation." It is believed that careful study, through cultures, of the plants of both sexual and apogamous species may throw some light on such questions as these. In whatever manner the ooapogamous condition arose, it was doubtless attended by an increase in the chromosome number, as will appear from the following table:

	Sexual forms		Ooapogamous forms	
	Haploid	Diploid	Haploid	Diploid
T. vulgare	——	——	13	26
T. confertum	8	16	——	——
T. erythrospermum	——	——	——	26–30
T. albidum	——	——	——	36–40
T. platycarpum	8	16	——	——

Perhaps the numbers under the ooapogamous forms should be spoken of as diploid and tetraploid, for it seems that the ooapogamous condition is attended by a doubling of the chromosome numbers. The higher figures may be inaccurate because of difficulties in making the counts of the small chromosomes, or the number may be irregular as an expression of the abnormal condition that exists. As Rosenberg (9) has pointed out, in all cases of ooapogamy in seed plants where chromosome counts are available, the ooapogamous species of a genus have a larger number of chromosomes than the sexual species, and the number is usually double. One striking exception occurs in the genus *Rumex*, which should be further investigated. The significance of this connection between ooapogamy and the doubling of chromosome numbers can be only a matter of speculation at the present time.

VARIATION IN TARAXACUM

Both *T. erythrospermum* and *T. vulgare* present great variability, and it is possible that the tendency to vary may be due to the large chromosome content. It would be interesting to know whether sexual forms with the 8 (16) chromosome-number show a similar tendency to variation. The literature gives us no evidence in this matter. With the chromosome content abnormally increased, one might expect mutations. Should a mutation arise there would be no difficulty of its maintaining itself as a definite line, since hybridization does not enter as a disturbing factor. At the beginning of this work, it was conjectured that possibly some of the various forms of our common dandelion were fixed and that they would come true to type in the following generation. While they are often referred to, the writer has failed to find anywhere in the literature an explanation of the true nature of these various forms of *T. vulgare* and *T. erythrospermum*. The polymorphous condition has often been noted but definite explanations are wanting. For example, Sturtevant has deposited in the Cornell University Herbarium eight collections of *Taraxacum vulgare*, which he puts into five different varieties, differing from one another through a wide range of characters. Are such as these to be considered as fixed varieties, are they to be considered as variations called forth only for the immediate generation by environmental conditions, or are they fluctuating variations that have their cause within the plant rather than in the conditions of its environment? More than that, since the two species seem in their variations to intergrade so that it is at times difficult to say whether a particular form belongs to the one species or to the other, is *T. erythrospermum* perhaps to be considered merely as one of the numerous forms, a little more distinct than others, of *T. vulgare?*

To help toward a solution of these questions, cultures of the plants were resorted to. Dahlstedt (2) has already called attention to the necessity of cultures in the study of species of the genus and describes seven new species on the basis of cultures carried on in the "Bergianischen Garten" at Stockholm. In the summer of 1916 eight plants, determined by the writer as *T. vulgare*, were collected. These represented types of the most striking forms commonly observed and were selected with a view toward getting the greatest possible differences in leaf characters, size, involucral characters, etc. One typical plant of *T. erythrospermum* was also included as No. 9 of the series. From each plant one well-matured head was selected and the seeds of this preserved until February, 1917, when they were sown in pans of sterile earth in the greenhouse. In April fifty plants from each of the nine types were planted in rows in rich garden loam. In spite of good soil and cultivation they grew but slowly during the first season. The rapidly-growing plants that one observes on lawns and in similar situations arise from old rootstocks. The seedlings do not come to flower the first year. They were covered during the winter and, in the following spring, started a rapid growth, developed to a large size and produced numerous flowers and blowballs during the season.

When the plants were quite young, the rosette leaves showed some variation in form, ranging from entire to deeply pinnatifid-runcinate. These variations did not follow the parent type forms but occurred among the members of the same race. As they grew older, greater uniformity resulted, and in the second season two distinct uniform types developed in the nine races. All the races, except No. 9 (collected as *T. erythrospermum*) and No. 6, gave plants that were striking because of their uniform conformance to one definite type, a large *T. vulgare* type with characters as commonly attributed in the keys, the leaves being up to 12 inches in length and the scapes up to 18 inches. So uniform were the foliage and flower characters that it was impossible to find the slightest variation to set one of the seven races off from the others. In striking contrast to these uniform rows were those of races No. 6 and No. 9. No. 9 had been selected as *T. erythrospermum* and gave a uniform race of plants somewhat larger than the parent plant but having the characters usually attributed to the species. Exactly like these plants were those of race No. 6, and it was a surprise to see that an error in determination had been made in the selection of this parent plant, a *T. erythrospermum* form having been mistaken for one of the *T. vulgare* forms, which only goes to show that the two so intergrade as to be sometimes, at least, indistinguishable. Sears (11) says, "both species possess such a wide range of forms that the only safe criterion for separating them seems to be achene color and form." And even these characters intergrade. There are dwarf forms of *T. vulgare* that have achenes conforming in shape, size, and spine characters to those of *T. erythrospermum.* The achene color varies from a light olive green to gray or brown and in some cases a red pigment is developed almost as distinct as in *T. erythrospermum;* while fruits of the latter species that have matured in wet or cold weather often lack the distinct red color. It would seem then that to be sure in all cases of the identity of a plant, one must resort to cultures. In fact, so polymorphous are many of the species of this genus that it would be desirable to grow the species together in order to determine just what typical forms result under certain uniform environmental conditions. From what the writer has seen of some herbarium material named *T. palustre* (Sm.) Blytt nothing would indicate that it was anything more than a form of *T. vulgare*, like one of the seven kept under cultivation. Fernald (3) speaks of the difficulty at times of separating *T. palustre* from *T. vulgare* and says the former occurs in "damp sheltered situations, especially roadside ditches and similar spots," and it is in such situations that a variety of *T. vulgare* can at times be found having more or less the characters usually ascribed to *T. palustre*. Herbarium material has been studied of American plants named *T. lividum* (Waldst. & Kit.) Heller, *T. mexicanum* DC., *T. oblanceolatum* A. Nelson, *T. officinale alpinum* Koch, and *T. laevigatum* (Willd.) DC.; and similar difficulties are presented. Sears (11) concludes that the last of these is identical with *T. erythrospermum*, but the writer would hesitate to come to this conclusion from the varying herbarium material. The plants should be seen growing side by side. Dahlstedt (2) says *T. erythrospermum* belongs to the *T. laevigatum* group, and that if the whole group were to be made one collective species, the latter name would apply as having priority. In the preparation of his excellent monograph of the genus, Handel-Mazzetti (4) studied herbarium material of most of the species described as new in America, especially from the Rocky Mountain region and Canada, and placed most of them under definite European species.

The writer would welcome specimens with seeds from any of the species of *Taraxacum* found in America, in order that he might grow these together under similar environmental conditions and make some definite determinations as to just how far soil and climate are responsible for the varietal and specific or supposed specific differences in this genus. Moreover, such a collection of plants in culture would make possible further cytological and genetical studies which it is planned to carry out. The cultures commenced in 1916 were interrupted during the two years of the war but are being resumed now.

MEGASPOROGENESIS IN TARAXACUM ERYTHROSPERMUM

The megaspore-mother-cell is a hypodermal cell at the apex of the nucellus and is easily distinguished by its denser staining. It rapidly increases in size, assuming an elongated form, and its large round nucleus attains a diameter not much less than that of a cross section of the cell. In the resting state, the nucleus show a large nucleolus (not more than one was ever observed) and a finely reticulate linin with densely staining chromatin. When entering the prophase, this reticulum becomes coarser by the merging of its elements, and the irregular strands soon contract into a dense mass—a typical synapsis (FIG. 1). Usually there are at the edges of the mass suggestions of threads, as appears in FIG. 1. Since this synaptic condition is encountered frequently in the preparations, it is reasonable to assume that it lasts a relatively long time. The spireme then loosens up until it is distributed again throughout the entire nuclear cavity. FIGS. 2 and 3 show stages in this process of loosening up, and FIG. 4 is drawn from a thin section of the nucleus when this stage is completed. The relatively thick thread appears to be of a finely granular nature. Nowhere in the preparations is there anything to suggest that the thread could be double at this stage. If it is a double thread, the two halves are so intimately merged as to be indistinguishable. In this stage *T. platycarpum*, which is a normally sexual species, is reported by Osawa (6) to present a clearly parallel spireme, while the ooapogamous species, *T. albidum* has a single spireme; neither does Juel (5) figure or describe a parallel spireme for *T. vulgare* at this stage. Osawa's figures seem very clear and definite in demonstrating the double spireme for *T. platycarpum*, and from the present known cases it would appear that the normal sexual *Taraxacum* species exhibit the double thread and the ooapogamous ones the single thread at the hollow spireme stage. It is interesting to note in this connection that Beer (1) doubts the existence of a double spireme at the hollow spireme stage in any of the Compositae that he has studied.

The thread now becomes shorter and thicker, the thickenings corresponding in number to the resulting number of chromosomes.

These thickened parts soon separate from one another (FIGS. 5 and 6) and are presently seen as irregular isodiametric chromosomes distributed throughout the nuclear cavity (FIGS. 7–9). At this stage counts are possible in thick optical sections. These counts vary from 26 to 30. No bodies are here observable that can be interpreted as its small nucleoli that Juel has described. The nucleus now gradually becomes elongated and, accompanying this elongation, the chromosomes undergo the remarkable change that Juel has described for *T. vulgare*, stating that it is a departure from all normal rules. This change consists in an elongation again of the chromosomes into irregular rod-shaped forms (FIGS. 10 and 11, the latter from a thin section.) These might be supposed to belong to earlier stages, like those shown in FIGS. 5 and 6, but the nature of the nucellus and the elongated form of the nucleus indicate that without a doubt this is a secondary elongation of the chromosomes after they had once assumed a more or less isodiametric form. The chromosomes here cannot be said to be in pairs except in so far as is brought about by chance, contrary to what Osawa reports for *T. albidum*. Nor does it seem possible that a splitting of the chromosomes here takes place, for there are certainly not upwards of 60 chromosomes in the nucleus at this time.

At this point the nucleus has become so much elongated that the larger dimension may be five times as great as the shorter (FIG. 12). The chromosomes again return to an isodiametric form and appear to be smaller and possibly denser bodies than when they first assumed this form. In the preparation from which FIG. 12 is drawn 31 chromosomes can be distinguished, though not with certainty. At this point the nucleolus and the nuclear membrane disappear, and one sees the spindle fibers make their appearance. The spindle is always regularly bipolar and in some cases is observed to lie at a considerable angle in the cell (FIG. 16). The wall between the resulting daughter cells is often also more or less oblique but never to so great a degree as was observed in the case of the spindle. Whether an abnormal shifting of the spindle was produced in some cases by fixation or other manipulation or whether the wall has a tendency to form in a position more nearly at right angles to the long axis of the cell is not known. The chromosomes are at first loosely scattered over the entire spindle (FIG. 14) but soon move toward the equatorial plane and are there arranged in quite regular order (FIGS. 13, 15 and 16). Meantime the spindle shortens somewhat and has all the appearance of a spindle in a vegetative cell. In fact, it is frequently possible to compare it with a spindle in the vegetative tissue of the ovule in the same preparation and, except for the somewhat smaller size of the latter, no difference is to be observed.

The chromosomes now separate into halves and the anaphase is quickly completed. FIG. 17 represents the completed division. In the daughter nuclei the chromatin becomes arranged into an indefinite network, but the chromosomes do not immediately lose their identity in this network but remain as irregular enlargements (FIG. 18). The nucellus at this time gradually disappears. No second division takes place to form a tetrad. The chalazal daughter cell quickly enlarges to form the mother-cell of the embryo-sac while its sister cell degenerates and is crowded into a gelatinous cap. (FIGS. 19 and 20). At this stage the pollen in the same flower is mature, but the loculi are still unopened.

A single division of the megaspore-mother-cell takes place also in *T. vulgare*, and the same condition has been reported in the ooapogamous *T. albidum* by Osawa (**6**); the sexual species, however, *T. platycarpum* (**6**) Osawa, and *T. confertum* (Rosenberg, **9**), show two divisions to produce tetraspores. From this it appears that with the loss of sexuality has gone the loss of one of the divisions of the megaspore-mother cell.

Material was fixed principally in Flemming's medium solution and stained with Flemming's triple stain, as used in Mottier's laboratory, though Haidenhein's haematoxylin method was also used. The use of turpentine, as recommended by Professor Mottier for bleaching after osmium fixers, was found almost indispensable in gaining clear preparations. My best thanks are due Professor Mottier for his kind help.

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Explanation of plates 6 and 7

All the figures were drawn with the camera lucida. FIGS. 19 and 20 are magnified about 800 diameters; the remaining figures, about 1800 diameters.

PLATE 6

TARAXACUM ERYTHROSPERMUM Andrz.

FIG. 1. Megaspore-mother-cell with nucleus at stage of synapsis.

FIGS. 2, 3. Chromatin coming out of synapsis as a single thread.

FIG. 4. Thin section at hollow spireme stage.

FIGS. 5, 6. Segmentation of the thread into chromosomes.

FIGS. 7–9. Optical sections of nuclei with short thick chromosomes.

PLATE 7

TARAXACUM ERYTHROSPERMUM Andrz.

FIG. 10. Secondary elongation of the chromosomes.

FIG. 11. Thin section at same stage.

FIG. 12. Second shortening and thickening of chromosomes just prior to spindle formation, nuclear membrane disappearing.

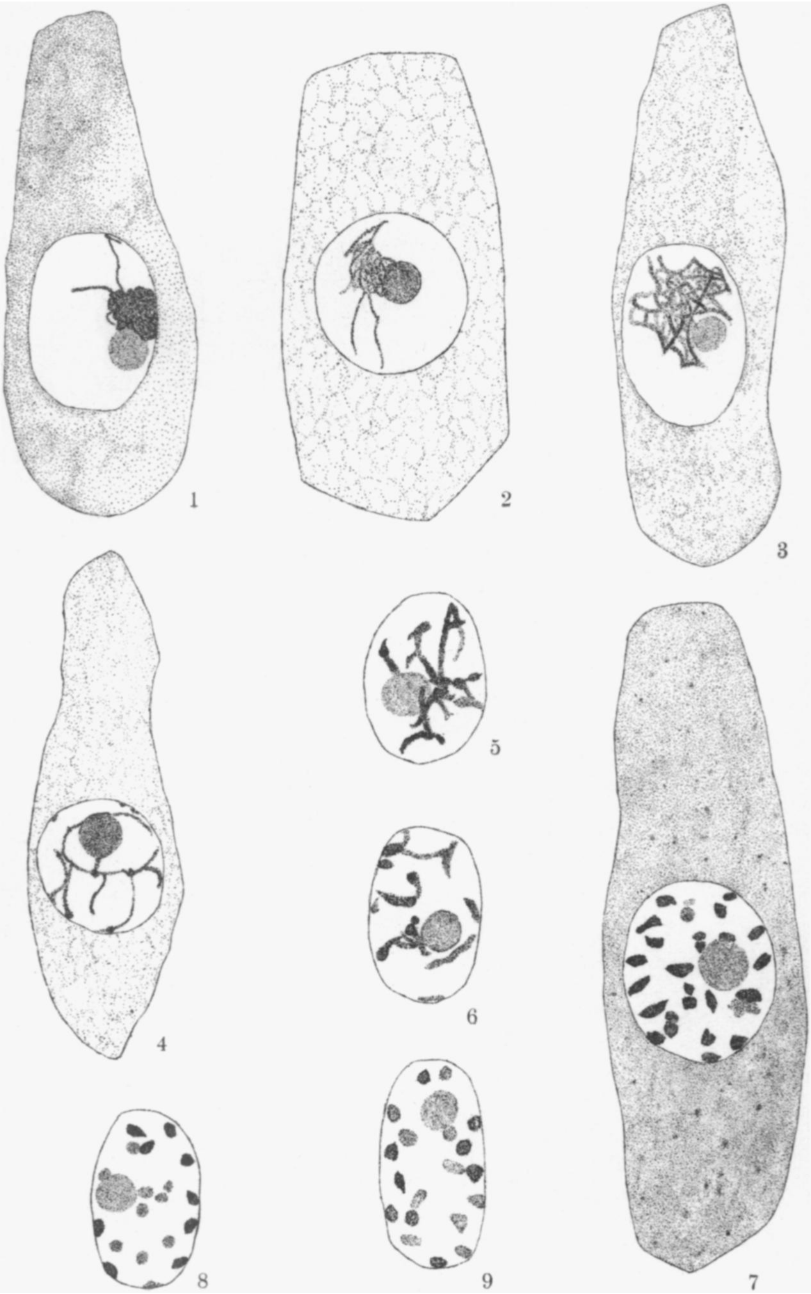
FIGS. 13, 14, 15. Arrangement of chromosomes on spindle.

FIG. 16. Characteristic regular metaphase stage; oblique position of spindle in cell.

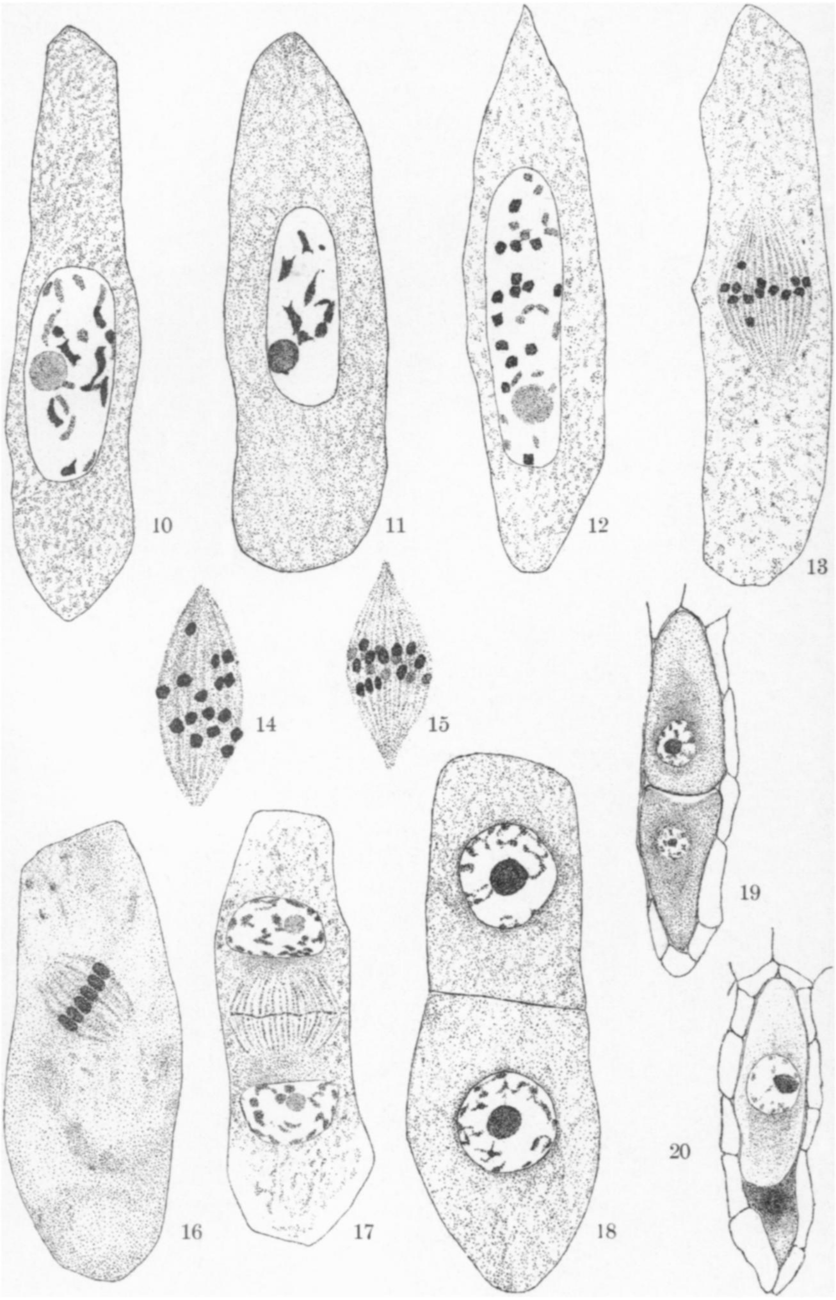
FIG. 17. Telophase with disappearing spindle.

FIG. 18. Daughter cells of first and only division.

FIGS. 19, 20. Later stages of same; upper cell in each case is the chalazal cell.



STORK: TARAXACUM



STORK: TARAXACUM